A COMPARATIVE ACCOUNT OF THE ACTIVITY OF DIFFERENT GROUPS OF SOIL INVERTEBRATES IN THE DECOMPOSITION OF FOREST LITTER*

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The role of soil invertebrates in the decomposition of forest litter is not confined to the mechanical disintegration of plant tissues. The decomposition of cellulose and rapid mineralization of plant cell contents occur in the gut of many animals (myriapods, woodlice, molluscs, enchytraeids). Primary humification of plant material is effected by several groups of invertebrates (earthworms, dipteran larvae). The composition of the animal population of forest litter determines the nature and rate of its decomposition.

The rate of decomposition of plant litter in forests of different types depends on the climatic conditions, the composition of the forest trees, and also on the activity of the soil microflora and fauna. The transformation of plant remains by animals is due primarily to the activity of saprophages, which constitute 70-80% of the total number of soil-dwelling multicellular invertebrates in soil (Gilyarov, 1960).

An account of the activity of soil animals is given in some large manuals of soil zoology (Tischler, 1965; Müller, 1965; Brauns, 1968). If we sum up this information briefly we obtain the following main aspects of the role of animals in the decomposition of plant remains:

1. By passing plant tissues through their gut animals reduce them to small fragments and thus produce a huge surface on which microbes and physical and chemical factors can act.

2. By means of their own enzymes and the enzymes excreted by symbiotic organisms invertebrates can digest some of the carbohydrates and other cell inclusions, thus liberating lignin, which forms a complex compound with cellulose.

3. One of the products of protein metabolism of many invertebrates is ammonia. Condensation of lignin with ammonia occurs in the gut of soil-dwelling animals and this greatly accelerates humification processes.

4. Digestion in the gut of soil invertebrates leads to partial mineralization of plant remains and, in some groups of animals, to partial humification also.

5. By their vertical migrations in the soil animals carry plant remains into the deeper soil horizons and bring about the mixing of organic and mineral particles. The movements of animals improve the aeration of the soil and stimulate the aerobic decomposition of organic matter.

The activity of soil animals is closely linked with the activity of the soil microflora and the functions of these groups are often intertwined. In many cases animals can only use plant remains if these remains have first been acted on by microorganisms. The excreta of animals in turn provide a suitable medium for bacteria and fungi and form centers of microbial activity in the soil (Stebaev, 1958; Kozlovskaja, 1969). Moreover, for some soil invertebrates, such as nematodes and microarthropods, the actual food is not the decomposing plant tissue, but the abundant microorganisms present in it. Thus,

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in the conversion of forest litter animals act, on one hand, as direct agents which bring about chemical and physical changes in the plant tissues, and, on the other, as regulators of microbial processes.

Many species of invertebrates colonize plant remains at particular stages of decomposition. The successions of invertebrates in rotting wood (Mamaev, 1960), in leaf mould, and forest litter (Chernova, 1966, 1969) have been described in detail. This indicates that particular processes of decomposition of forest litter involve different groups of animals.

The composition of the soil fauna includes 15 classes of invertebrates. It is quite obvious that in the complex, many-stage processes of decomposition of plant remains different groups of animals will perform different functions. Among the soil-dwelling saprophages Dunger (1958, 1963) distinguishes "primary" and "secondary" destroyers of plant remains. In the first group he includes the representatives of the soil mesofauna, which can consume and destroy tough plant remains without decomposing them structurally or chemically. The secondary destroyers are members of the soil microfauna, which can only feed on plant tissues after they have been fragmented by the large invertebrates. In Dunger's opinion, the primary destroyers mainly effect mechanical disintegration of the litter, while the activity of the secondary destroyers is responsible for the chemical changes in plant tissues. However, investigations of the feeding and digestion of soil invertebrates of various groups show that the activity of saprophages does not fit into this scheme. Below we give an account of the activity of some groups of soil invertebrates which are common in the mixed woods of Central Europe and the USSR.

Earthworms. The role of earthworms in the conversion of organic matter has been known since Darwin's time and their activity has been investigated by many scientists. The litter is acted on by worms living in the litter, in the top layers of soil, and also by worms which live deeper in the soil, but which tunnel up to the soil surface. Some species can feed on litter, which they drag down into the soil, while others consume the minute plant tissue particles which are dispersed in the mineral mass of the soil after their primary conversion by other animals and microorganisms. Thus, worms include primary and secondary destroyers.

Worms are selective towards litter from different trees and shrubs. For instance, Lumbricus terrestris shows greatest preference for elder and elm, and least for coniferous and oak litter (Satchell and Lowe, 1967). In some regions with a mild and moist climate, however, earthworms play an important role in the decomposition of conifer litter (Wittich, 1953; Zachariae, 1967).

In the gut of earthworms plant tissues are partially humified and converted to "clay–humus" complexes, which are the basis of stable humus (Meyer, 1943). In addition to plant remains worms ingest mineral soil particles and mix them together. Wormcasts are highly resistant to water and provide a basis for the creation of soil structure (Ponomareva, 1953). The active mixing of forest litter with soil by earthworms leads to the formation of a typical forest soil profile (see Perel' and Sokolov, 1964; Perel et al., 1966).

Earthworms actively destroy rotting wood on the surface of soil. The tunnels of worms enter rotten tree stumps from the soil and pass right through them to the top (Wilcke, 1953). The feces of worms from wood contain large amounts of humic acid and fulvic acid (Striganova, 1968).

Myriapods. Among the large invertebrates diplopods (millipedes) play an important role in the decomposition of leaf litter in forests. The number of millipedes in the deciduous forests of some moderate and warm regions is fairly large – up to several tens per m^2. In the North Caucasus millipedes destroy up to 100 kg of litter per ha on the average per month (Striganova, 1969b). In the forest of the Lenkoran region of Azerbaidzhan millipedes pass through their gut in a month 250-300 kg of litter per ha (Striganova, 1970). In the forest belts of Lugansk region, where the dominant millipede is Sarmatiulus kessleri, the myriapods, according to our data, destroy 80-90 kg of litter per ha daily.

Microscopic investigations of the gut contents and feces of millipedes show that plant tissues digested by these invertebrates are half macerated (Striganova, 1967). It has been believed for a long time that millipedes only comminute leaf litter, but assimilate very little of it, and hardly alter its chemical composition at all (Van der Drift, 1951; Gere, 1956; Dunger, 1958). It has been suggested that millipedes feed mainly on fungal hyphae and bacteria which colonize rotting leaves. Our experiments showed that the degree of assimilation of litter by millipedes is fairly high – 20 to 60%. For instance, the degree of assimilation of oak litter and hornbeam litter by Pachyiulus foetidissimus is 37.6% and 39.4%, respectively (Striganova, 1969a). The degree of assimilation of oak litter and ironwood litter is 32% and 43%, respectively (Striganova, 1970).

Millipedes have a rich assortment of enzymes in their gut. Nielsen (1962) established the presence of various carbohydrases (invertase, maltase, amylase, etc.). We also found high cellulase activity in the mid and hind gut of millipedes (Striganova, 1970). This suggests that millipedes can digest cellulose. A comparison of the cellulose content of litter on which millipedes were feeding and their feces showed that the amount of cellulose decomposed when these animals fed on hornbeam, maple, oak, and beech litter was 40%, 70%, 87%, and 72%, respectively. The absolute amounts are 3-5 mg of cellulose per day. The decomposition of the walls of plant cells allows rapid digestion and assimilation of their contents by the millipedes, and the final metabolic products are readily mineralized. It has been shown that the ash content of millipede feces is higher than that of their food (Sokolov, 1955; Byzova, 1970).

Millipedes do not move down deeply into the soil. Their feces remain on the surface, rapidly disintegrate, and are decomposed by rain and microbial activity.

Woodlice. Woodlice, which can skeletonize leaves, form an active group of primary destroyers of leaf litter. Woodlice sometimes colonize rotting wood and actively convert it (Striganova, 1968). In addition, some species of fungi serve as food for woodlice (Müller and Beyer, 1965). There is no direct evidence that woodlice destroy cellulose, but cellulase has been found in their gut (Hartenstein, 1964). Woodlice in forests are active only in the litter and at the soil surface (Anufrieva, 1963). Thus, in the invertebrate complexes which colonize the forest litter woodlice are similar in their activity to millipedes.

Dipteran Larvae. Fly larvae which develop in forest litter are known to be active consumers and destroyers of litter. Larvae of Bibionidae, Tipulidae, Lycoriidae, and Sciophilidae develop in forest litter. They inhabit the lower layers of litter and feed on the moist soft litter which has been acted on by microorganisms. The feces of large flies provide food for small fly larvae and enchytraeids (Zachariae, 1965). Rapid decomposition of cellulose and mineralization of plant material occur in fly feces (Brauns, 1954; Dunger, 1963; Zachariae, 1965). In addition, litter is partially humified in the gut of some forms of symbiotic microorganisms (Kononova, 1944; Priesner, 1961; d'Aguilar and Bessard, 1963; Karpachevsky, Perel, and Bartsevich, 1968). Thus, dipteran larvae, like other primary litter destroyers, accelerate the mineralization of litter but, as distinct from myriapods and woodlice, these insects also effect the initial stages of humification of plant remains, which is subsequently completed by microorganisms.

Enchytraeids. These worms are widely distributed in deciduous and coniferous forests and occur in large numbers in the litter and top layer of soil. Their numbers vary from a few tens of specimens to several tens of thousands per g of soil (Jegen, 1920). The feeding of enchytraeids and their role in the decomposition of forest litter has been investigated thoroughly by Zachariae (1964, 1965). He distinguished a group of primary destroyers which can skeletonize leaves, and a group of secondary destroyers which feed on the feces of millipedes and dipteran larvae. It is the last group which is of practical importance in forests. These enchytraeids dwell in the bottom layer of litter and on the soil surface. They can digest only comminuted and macerated particles of plant tissue. In some forests the feces of enchytraeids form an entire layer between the soil surface and the litter. Their feces contain hardly any cellulose. Enchytraeids apparently finish off the decomposition of cellulose initiated by other animals. This is of particular importance in coniferous forests, where the numbers and activity of large invertebrates are low and cellulose constitutes the bulk of the moder (O'Connor, 1967).

Collembola. Some representatives of this order are active primary destroyers of litter. When present in large numbers they play an important role in the mechanical disintegration of litter. Soudek (1928) calculated that 20 thousand Collembola produce 480 ml of feces per day. Collembola are of particular importance when larger destroyers are absent. For instance, in the tropical forests of Nigeria, where Collembola and mites are the dominant groups in litter, they very rapidly effect the entire work of disintegration of the litter (Madge, 1965).

Some researchers think that Collembola feeding on litter play a role in the humification of litter and that their feces form a humified mass of the mull type (Schaller, 1950; Poole, 1959). Microscopic and chemical investigations of the feces, however, do not confirm this opinion. Brauns (1968) points out that Collembola reduce plant tissue to fine particles, but they hardly alter its chemical composition and they do not decompose cellulose. The investigations of Zachariae (1963, 1965) showed that the food of Collembola consists mainly of bacteria and fungal mold. They also consume the decaying corpses of invertebrates in the soil. Thus, Collembola are only mechanical destroyers of forest litter. The successional changes in the Collembola complex during the decomposition of litter are presumably due to changes in the microflora.

TABLE 1

Invertebrate groups in forest litter	Mechanical destruction of litter	Cellulose decomposition – mineralization	Primary humification
Collembola	++		
Oribatei	+++		
Diplopoda	+++	+++	
Oniscoidea	+++	+++	
Mollusca	+++	+++	
Enchytraeidae	++	+++	
Diptera (larvae)	+++	+	+
Lumbricidae	+		+++

+ — effected by individual species;
++ — effected by group of species;
+++ — effected by most or all species.

Acari. Like Collembola, acari are sometimes abundant in the upper layers of litter in deciduous forests and act as primary destroyers of litter (Witkamp and Crossley, 1966). Large numbers of acari inhabit the lower layers of litter, which contain comminuted plant remains, and feed on the feces of other invertebrates (Schuster, 1956). There is no humification or appreciable mineralization of litter in the gut of acari. Acari assimilate only easily digestible compounds – proteins, some carbohydrates, and lipids. They do not digest cellulose or lignin. Hence, acari, like Collembola, are significant only as mechanical destroyers of litter. It is important to note that acari accomplish deep vertical migrations in the soil and transport organic matter into the deep horizons.

Nematodes. Nematodes occur in vast numbers in decaying plant remains, including forest litter. They feed on plant and animal material, but they use only the cell protoplasm and they cannot digest cell walls (Nielsen, 1967). Hence, nematodes do not take part in the decomposition of plant remains and have no effect on the mechanical and chemical decomposition of litter. Nematodes which feed on bacteria may control to some extent the specific composition of the microflora and the relative numbers of particular species of microorganisms. Nematodes in abundance in plant remains play a role in the cycle of substances by dying off and forming a nitrogen-rich substrate in which decomposition processes are particularly rapid (Meyl, 1961; Stöckli, 1952; Palissa, 1964).

This review of the activity of different groups of invertebrates indicates the great differences in their functions in the decomposition of forest litter. If we consider only those processes which are directly associated with the functions of animals, we can distinguish three categories of processes in the activity of the soil fauna: 1) mechanical disintegration of plant tissues; 2) decomposition of cellulose and mineralization of plant tissues; 3) primary humification of plant remains. The participation of different groups of animals in these processes is shown in the table.

Acari and Collembola take part only in mechanical destruction of litter. Millipedes, woodlice, molluscs, and enchytraeids not only actively fragment litter, but they also decompose a large part of the cellulose in plant tissues and stimulate mineralization of plant remains. Some groups of dipteran larvae also assist in the mineralization of litter. Primary humification of litter occurs in the gut of certain dipteran larvae. Finally, earthworms play an active part in the humification of plant material. Worms, by feeding on litter, also effect its mechanical destruction.

Thus, soil invertebrates are implicated in all the main stages of decomposition of plant remains. The composition of the animal population of forest litter determines the nature and rate of its decomposition. The diversity of the species and group composition of the invertebrate fauna of forest soils ensures the most rapid decomposition of plant remains and the formation of a high-grade humus.

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